

# **16 Insularity and micromammal-macroparasite relationships**

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## **1 Introductory remarks**

### **1.1 Micromammals and the insular syndrome**

Island biogeography has been extensively studied since the pioneering studies of MacArthur and Wilson (1963, 1967), followed by numerous studies showing the magnitude and direction of ecological and evolutionary processes that operate within and among insular populations, species and communities. Insular trends have been extensively studied in terrestrial vertebrates, especially in lizards, birds, and mammals (e.g., Stamps and Buechner 1985). The cascade of changes that affect the life-history traits of insular populations is sometimes called “insular syndrome”. Despite the fact that a great number of environmental factors may vary among different islands, the main components of the insular syndrome can be summarized as morphological, behavioural, demographic, ecological, physiological and genetic shifts exhibited by organisms living in isolation (Blondel 1995). Indeed, all levels of biological organization, from individuals to interactive communities, are under the effects of the insular environment.

Insular faunas are characterized by an impoverishment in species number. Species with good dispersal ability, being generalist or abundant on the mainland are favoured on islands (Sarà and Morand 2002). As a consequence, there is a decrease in interspecific competition and in predation pressure often associated with some demographic and ecological changes: density increase, ecological niche widening, resistance to invasions, and greater vulnerability to perturbations (Alder and Levins 1994; Blondel 1995). Insular small mammals show also a decrease in litter size (Fons et al. 1997), an increase in adult survival and often also a decrease in aggressiveness (Alder and Levins 1994).

At the same time, morphological changes divide insular mammals into two main evolutionary groups so that small species (<100g) tend to become larger (gigantism), whereas large species (>100g) tend to become smaller (dwarfism) (Van Valen's rule; Van Valen 1973; Lomolino 1985). Patterns of variation in body size of insular mammals seem to support the hypothesis that, based on physiological arguments, the optimal body mass for a terrestrial mammal is approximately 100 g (Brown 1995; Meiri et al. 2004). Finally, changes in energy expenditure in insular mammals have also been observed (Arends and McNab 2001; Magnanou et al. 2005).

## 1.2 Macroparasites on islands

Studies analysing selective forces that may drive evolutionary changes on islands generally consider resource abundance or competition and predation pressure release but too often ignore parasitism (Michaux et al. 2002). However, the "insular syndrome" should also affect parasites and host-parasite interactions.

First, new environmental conditions linked to an impoverishment in free-living species richness could obviously have consequences on the structure of parasite assemblages. Several studies showed that the macroparasite fauna of a given host species can strongly differ between mainland and island populations (Thomas 1953; Mas-Coma and Feliu 1984; Mas-Coma et al. 1988; Goüy de Bellocq et al. 2002). This difference involves the richness in parasite species, their identity (depending on mainland abundance or life cycle) but also their specificity (see review in Combes 1995).

Second, parasites may be affected by the life-trait shifts of their mammal hosts. Changes in mammal density, mammal body size and/or behaviour should have direct consequences on the epidemiological parameters (prevalence and intensity) (Mas-Coma et al. 2000). The effects of the decrease in mammal genetic diversity (Frankham 1997) on their parasites are even less known (Table 1).

As a consequence, changes in selective forces may affect the evolution of insular host-parasite interactions as theoretically predicted by Hochberg and Møller (2001). An increasing number of studies have demonstrated that parasites play an important role in host ecology, immune investment, population dynamics, behaviour, energy allocation, etc (Gregory 1991; Hudson et al. 1992; Newborn and Hudson 1992; Lindstrom et al. 2004), so it seems relevant to identify and quantify the effect of modified parasite assemblages on the ecology and evolution of insular micromammals.

**Table 1.** Interactions between hosts and parasites in relation to the insular syndrome. (M: micromammals, P: parasites)

Micromammals	Parasites	References
Decrease in species number	Decrease in species number	M: MacArthur and Wilson 1963, 1967 P: Thomas 1953; Mas-Coma & Feliu 1984; Gouy de Bellocq et al. 2002, 2003
Nested patterns	Nested patterns	M: Sarà and Morand 2002 P: Gouy de Bellocq et al. 2003
Generalist species	Direct life cycle species	M: Blondel 1995 P: Gouy de Bellocq et al. 2002
Density increase	Abundance increase	M: Alder and Levins 1994 P: Mas-Coma et al. 2000
Decrease in intraspecific competition	Decrease in intraspecific competition	M: Alder and Levins 1994 P: Mas-Coma et al. 2000
Ecological niche widening	Host capture	M: Cheylan 1988 P: Théron and Pointier 1995
Dwarfism and gigantism (100g threshold)	Shifts in parasite body size	M: Van Valen 1973 P: Valéro et al. 1996
Decrease in fecundity and increase in longevity	Parasite demography?	M: Fons et al. 1997; Alder and Levins 1994
Decrease in genetic diversity	Decrease in genetic diversity	M: Frankham 1997 P: Nieberding et al. 2006
Decrease in immune defence investment	Decrease in parasite diversity	Lindstrom et al. 2004
Impact on host fitness	Decrease in virulence	Hochberg and Møller 2001

### 1.3 Macroparasite contributions

This chapter illustrates to what extent parasites have to be considered in island biogeography, as parasites may have an influence on host evolution in addition to other selective pressures. We present an overview of the knowledge concerning micromammal parasite faunas on islands, focusing on two rodent species, namely the woodmouse *Apodemus sylvaticus* and the black rat *Rattus rattus*. Specifically, we first discuss the issues related to species richness and parameters that may influence it. The second part

of the chapter deals with parasite host specificity and focuses on two well-known examples of parasite transfer occurring in an invasive host species on an island (*Fasciola hepatica* and *Schistosoma mansoni* in *R. rattus*). These examples may be relevant for (1) understanding host and parasite invasion processes; (2) management as some parasites considered here have veterinary and public health importance; and (3) conservation as endemic free-living species are especially vulnerable to perturbations caused by invaders.

## **2 Patterns of macroparasite species richness and abundance on islands**

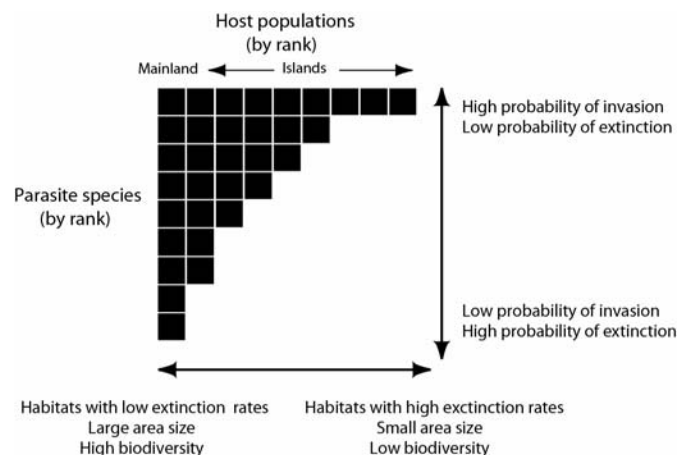
### **2.1 Nestedness**

A nested pattern in the assemblages of both free-living organisms and parasites is often the rule. Species in depauperate assemblages generally constitute subset samples of richer assemblages (Patterson and Atmar 1986; Poulin 1996; Poulin and Guégan 2000; Krasnov et al. 2005). Nested patterns, mainly investigated in species assemblages living in fragmented or insular habitats, are considered to be a result of colonisation and extinction processes. Goüy de Bellocq et al. (2003) showed that nestedness does occur in the parasite community of *A. sylvaticus*, and that this pattern can be related to the parasite life cycles and to the host geographic distribution (mainland versus islands, large versus small islands) (Fig. 1). Goüy de Bellocq et al. (2003) suggested that parasite species at the top of the presence/absence matrix are those with high probabilities of colonization and low probabilities of extinction, whereas parasite species at the bottom of the matrix are those with properties resulting in low probabilities of colonization and high probabilities of extinction. These properties reflect the parasite life-style: direct versus indirect life cycle, high versus low host specificity.

Parasite species found on small islands are subsets of larger assemblages found on larger islands or on the mainland. Hosts that have succeeded in establishing themselves on an island do not harbour the whole parasite community that is observed in the mainland host populations, but a specific subset of parasite species. Indeed, even if hosts succeed on an island, their parasites have to meet the conditions allowing them to survive. These include, for example, presence of suitable intermediate or definitive hosts and/or environmental conditions that permit the survival of free-living stages. Thomas (1953), Combes (1995) and Goüy de Bellocq et al. (2003)

showed that indirectly-transmitted parasites have a lesser chance of establishing themselves on islands than directly-transmitted parasites because of the poverty of free-living species encountered there. Parasites that need three hosts with an aquatic phase for their transmission are generally considered to have the lowest chance to invade an island. For example, Goüy de Bellocq et al. (2003) observed a lack of trematode and cestode species with complex life cycles on both continental and oceanic islands. Trematodes and acanthocephalans are usually found on large but not on small islands (Mas-Coma et al. 1984, 2000; Jiménez Piqueras 1992; Goüy de Bellocq et al. 2002, 2003).

Host populations live on islands that differ in biodiversity and ecological stability. Hence, according to the matrix model, islands at the left of the matrix may be characterized by their low extinction rates, high biodiversity and/or large area size and islands at the right may be characterized by their high extinction rates, low biodiversity and/or small area size (Fig. 1).

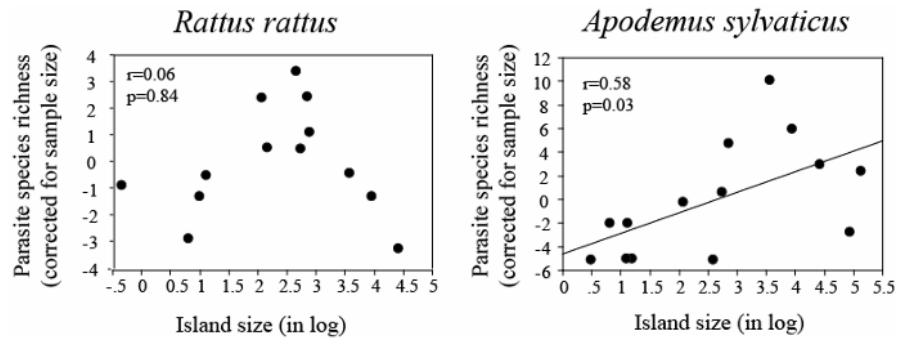


**Fig. 1.** Nested patterns of parasites in relation to insularity (adapted after Goüy de Bellocq et al. 2003)

## 2.2 The effect of island size

As mentioned above, islands are characterized by a dramatic reduction in species richness compared to mainland areas of similar size (MacArthur and Wilson 1967). Likewise, parasite faunas exhibit a marked decrease in species number on islands (Thomas 1953; Mas-Coma and Feliu 1984; Goüy de Bellocq et al. 2002). However, the relationship between parasite species richness and island size is far from being universal. The non human-associated *A. sylvaticus* follows this rule: the smaller the island, the

lower the parasite species richness. However, this relationship is not observed with the human-associated and invasive *R. rattus* (Fig. 2).



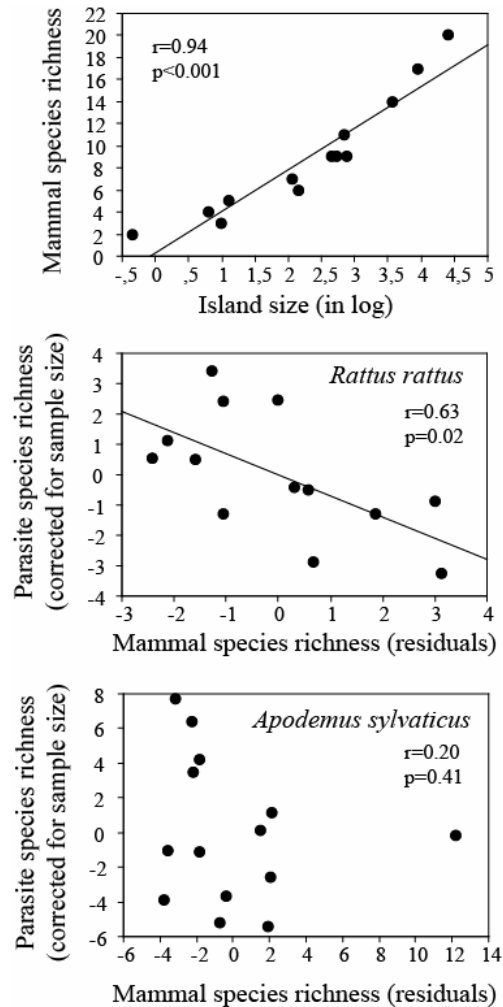
**Fig. 2.** Relationship between the size of the island and parasite species richness in two rodent species, *Rattus rattus* and *Apodemus sylvaticus* (modified after Gouïy de Bellocq et al. 2002, 2003 and Gouïy de Bellocq and Morand, unpubl. data)

### 2.3 The effect of insular host diversity

Insular biotope diversity, biological diversity and ecosystem stability should play important roles in the richness, structure and composition of parasite assemblages. Esteban Sanchis (1983) recorded the parasite fauna of the lesser white-toothed shrew *Crocidura suaveolens* on the mainland and Mediterranean islands. The impoverishment in larval cestodes was lower on Corsica than on Minorca or Porquerolles, reflecting a lower abundance of predators of the shrew (which are the definitive hosts of these cestodes) on Minorca than on Corsica (Esteban Sanchis 1983).

Nieberding et al. (2005b) observed a positive relationship between the mammal species richness and the parasite species richness of *A. sylvaticus* on Mediterranean islands. However, when mammal species richness was controlled for island size (i.e. for the area/diversity allometry), this relationship disappeared (Fig. 3). The parasite species richness of *A. sylvaticus* is independent of the residual variation in mammal diversity, which may indicate a saturation of the parasite community.

In contrast to *A. sylvaticus*, a negative relationship is observed between the residuals of mammal species richness and the parasite species richness of *R. rattus*. This may indicate that the parasite communities of insular *R. rattus* were far from being saturated, and that niches are open for new parasites. Empty niches may explain why parasite capture and lateral transfer are often recorded from *R. rattus* when colonizing new islands (see below).



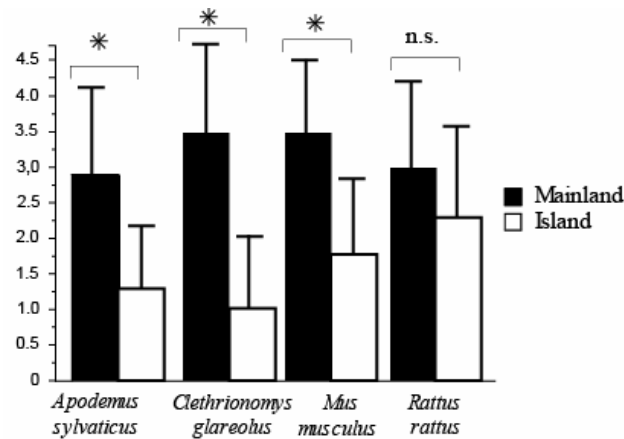
**Fig. 3.** Mammal diversity in relation to island size, and relationship between parasite species richness and mammal species richness (controlled for island size) in two rodents, *Rattus rattus* and *Apodemus sylvaticus* (data from Göüy de Bellocq et al. 2002, 2003 and Göüy de Bellocq and Morand, unpubl.).

#### 2.4. Insularity and host specificity

Many parasites cannot become established on an island because of the complexity of their life cycles, and/or the environmental conditions and the hosts needed for their survival. It has been repeatedly shown that host

specificity, i.e. the number of host species per parasite species, significantly decreases on islands (see Combes 1995 for review).

Goüy de Bellocq et al. (2002) investigated mean host specificity of parasites exploiting four species of hosts from the insular versus mainland populations. They found that parasites of three host species demonstrated a significant decrease in their host specificity on islands. This was explained by the decrease in the richness of mammal communities that may prevent the installation of host specific parasites. This, however, was not the case for parasites of *R. rattus* that demonstrated no difference in their host specificity on islands compared to the mainland, suggesting that *R. rattus* is able to exchange many parasites with other insular mammals as well as to acquire new parasites from them. The reason for this could be the broadening of the rat's ecological niche on islands (Cheylan 1988).



**Fig. 4.** Mean number of host species exploited by a parasite species harboured by individuals of four rodent species from mainland and island populations (data from Goüy de Bellocq et al. 2002)

## 2.5 Anthropic factor

The above examples show that the pattern of parasite species richness does not always fit with the predictions of the island biogeography theory related to species-area relationship, isolation, or life cycle. On the one hand, patterns demonstrated by parasites of the non-human associated *A. sylvaticus* could be well explained by the insular paradigm. On the other hand, this appeared not to be the case for the parasites of synanthropic rodents (*Mus musculus* and *R. rattus*) (Goüy de Bellocq et al. 2002).

Mediterranean islands were and are still at the crossroad of human migrations and commercial routes. All civilizations that succeeded on islands



have introduced many plants and animals, including micromammals (Dobson 1998). Several studies have shown that insular species may come from farther regions as a consequence of human activities (Lo Brutto et al. 2004; Cosson et al. 2005). As humans have facilitated the introduction of mammals, the effect of the distance to the closest mainland should be drastically diminished. In other words, geographic distance is unlikely a potential factor that may influence the parasites associated with synanthropic species. Moreover, because of these human introductions, mammal species richness could be higher on some Mediterranean islands than predicted by the species-area equilibrium (Vigne 1998) due to a bias towards invasion, even if the overall diversity has decreased with several extinctions of insular endemic species due to these introductions. This implies that many more parasites, especially generalist parasites, can find the ecological conditions (i.e. hosts) necessary to their establishment and spread. Moreover, inferring modifications of the insular parasite faunas, based on a comparison with the closest mainland, may introduce bias as the nearest mainland is not necessarily the source of the invaders to a given island.

## **2.6 Macroparasite richness and composition illustrate ecological and historical phenomena**

Parasites help understand host ecology, including trophic, competitive, phylogenetic or phylogeographic relationships between species (Mas-Coma and Feliu 1984; Nieberding et al. 2005a, 2006a; this volume).

For example, the parasite fauna of the greater white-toothed shrew *Crocidura russula* is markedly impoverished on the Mediterranean island of Ibiza compared to the closest mainland. Some parasites abundant in the European mainland, such as *Parastrongyloides winchesi*, are absent on Ibiza or restricted to few localities (Mas-Coma and Feliu 1984). On the contrary, *Brachylaima simoni*, *Gongylonema* spp., which are supposed to be of North African origins are common and abundant on Ibiza. Based on the parasitological data, Mas-Coma and Feliu (1984) concluded the insular population of this shrew is of African rather than European origin. More recently, molecular studies confirmed this hypothesis (Lo Brutto et al. 2004; Cosson et al. 2005).

## **3 Parasite invasion and lateral transfers on islands**

A lateral transfer implies a host change, or switch to a new host that was never before infected by a given parasite, and occurs usually after an intro-

duction into a new environment (Combes 1995). Several cases of lateral transfers have been observed on islands. For example, *Gongylonema brevispiculum* and *Streptopharagus kutassi* are found respectively in *A. sylvaticus* and *R. rattus*, on the Mediterranean island of Ibiza. The geographical origin of these two parasites is North Africa, where they parasitize Gerbillidae absent in Ibiza (Mas-Coma and Feliu, 1984).

The best-documented examples of lateral transfer on islands concern two trematode species: the liver fluke *Fasciola hepatica* on Corsica and *Schistosoma mansoni* in the Caribbean archipelago. The adult stages of these parasites were introduced by their definitive hosts, Bovidae and humans, respectively.

### **3.1 *Fasciola hepatica* and *Rattus rattus* in Corsica**

The liver fluke *F. hepatica* has a very broad spectrum of definitive hosts including livestock, wild animals (Lagomorpha, Marsupialia and Cervidae) and humans (Spratt and Presidente 1981; Menard et al. 2000; Shimalov and Shimalov 2000; Rondelaud et al. 2001). This parasite has a complex life cycle and uses freshwater molluscs as intermediate hosts. Host specificity of the fluke varies geographically (Hurtrez-Bousses et al. 2001). Although rats are only occasionally infested by the liver fluke all over the world (Li 1952; Molan and Hussein 1988), high prevalence of this parasite in *R. rattus* on the Mediterranean island of Corsica has been reported (Mas-Coma et al. 1988).

While typically commensal and omnivorous on the mainland, the black rat becomes more definitely wild (less human-associated) and markedly herbivorous on islands (Cheylan 1988). On islands, this species is a habitat opportunist. Furthermore, *R. rattus* is the most abundant small mammal on Corsica. Thus, the black rat represents one of the extreme examples of insular enlarging of an ecological niche so far reported for a mammal. The infestation by *F. hepatica* appears to be related to these changes in ecological characteristics and feeding behaviour of the black rat.

#### **3.1.1 Epidemiological context**

On Corsica, all localities with *F. hepatica* present in black rats are humid natural habitats that are used as pastures for cattle and sheep. These pastures also constitute favourable habitats for both *R. rattus* and the intermediate snail host (Fons and Magnanou 2004). In these localities, the prevalence of the liver fluke in the black rat is high (on average, 58% of rats were found to be infested by the parasite) without seasonal variation

(Magnanou 2005). Prevalences of various trematodes in small mammals in other regions are usually much lower (Ribas et al. 2005).

### **3.1.2 The effect of lateral transfer on host physiology**

Helminth parasites sometimes have a sharp negative effect on their vertebrate hosts (Connors and Nickol 1991; Kristan and Hammond 2000, 2001). This is also the case for *F. hepatica* (Dan et al. 1981; Smithers 1982; Mas-Coma and Bargues 1997). In particular, parasitism by the liver fluke increases the energy expenditure of the black rats (Magnanou et al. 2006). Resting metabolic rate of infected rats was always higher than that of unparasitized rats independently of the ambient temperature. Differences in mass specific energy expenditure between infected and uninfected rats were maximal at the lowest ambient temperature (when thermoregulation constraints were also at their maximum). There can be various mechanisms explaining the increase in the energy requirements of parasitized hosts (see Degen, this volume). Kristan and Hammond (2000, 2001) demonstrated that the presence of an intestinal helminth decreases the intestinal glucose transport capacity. Likewise, bile duct inflammations and necroses of liver tissues due to *Fasciola* infection have been reported. The trematode alters the function of the gall bladder and ducts and reduces digestion capacity (Chen and Mott 1990; Mas-Coma and Bargues 1997).

The most important finding of the study on the metabolic effect of liver fluke parasitism is that the increase in energy requirements caused by the fluke infection in black rats appeared to be extremely high (56%; Magnanou et al. 2006) compared with that of, for example, mice infected with *Heligmosomoides polygyrus* (9%; Kristan and Hammond 2000, 2001). This unexpectedly high increase in energy requirements may reflect the unusual situation experienced by both host and parasite.

### **3.1.3 Adaptations of the parasite**

Although the liver fluke can develop in *R. rattus* (Mas-Coma et al. 1987, 1988; Valero et al. 1998, 2002), murids are the smallest natural definitive hosts known for this parasite. Their small size may account for the numerous constraints experienced by the fluke. Indeed, *F. hepatica* eggs shed by murids are smaller than those shed by infected cattle (Valero et al. 2002). Adult body size at sexual maturity is smaller in flukes harboured by Corsican black rat than that of flukes harboured by cattle (Valero et al. 1996). Finally, liver flukes coil up in the bile duct of murids, whereas they do not coil in other, larger definitive hosts (Valero et al. 1998, 2002).

### **3.1.4 Delay in the co-adaptation**

Cattle and sheep were introduced to Corsica by humans about 7 000 years ago. *R. rattus* was introduced more recently (Vigne 1992). If this scenario is correct, the interaction *R. rattus*–*F. hepatica* from an evolutionary point of view is relatively young. This interaction seems to be established on Corsica due to precluded compatibility and shifts in host behaviour that, in turn, allowed the transfer of the parasite from cattle to the black rat. At present, an adaptation of the parasite to its new hosts seems to be already established, whereas adaptation of the host to its new parasite seems to be delayed. Indeed, the resistance of black rat against the liver fluke seems to be relatively low as suggested by high prevalences and high energetic costs imposed by the parasite (Magnanou et al. 2006).

## **3.2 Schistosoma mansoni and Rattus rattus in the Caribbean islands**

*S. mansoni* is a causative agent of human intestinal schistosomiasis. It is widely distributed in the tropical zone, and affects several hundred million people. *S. mansoni* was introduced to America during the slave trade. The parasite found an appropriate local intermediate mollusc, *Biomphalaria glabrata*. This allowed *S. mansoni* to become established and to spread in various parts of Central America, South America and in the Caribbean archipelago.

### **3.2.1 Epidemiological processes in a heterogeneous environment**

The epidemiology of *S. mansoni* on the island of Guadeloupe (West Indies) has been studied in great details by Théron and Pointier (1995). The transmission dynamics differed among three main eco-epidemiological systems, namely the urbanized, the marshy forest and the sylvatic foci (Théron and Pointier 1995). In the urbanized foci, humans were principal definitive hosts and the black rats were exploited by the parasite only occasionally, in localities where prevalence in humans was high. In the localities where both rats and snails were present, but humans absent, the black rats were never infected. In the marshy forest focus, characterized by scattered human settlements, prevalences of infection in the black rat were high (50-87%). The same was true for the intensity of infestation attaining 500 worms per rat. In other words, both humans and rats were equally involved in the transmission dynamics and the black rat was able to maintain the infection. In the sylvatic focus, where the rat population density was especially high, black rats were heavily infected with prevalences higher

than 60%. Thus, the rodent was the only definitive host able to maintain the infection in the focus where humans were absent (Morand et al. 1999).

### **3.2.2 Origin of lateral transfer**

*S. mansoni* has increased its host range (from 1 to 2 hosts) on the island of Guadeloupe following the introduction of the black rat. However, the Norwegian rat *Rattus norvegicus* was also introduced to the island without any implication of this rodent in the parasite transmission. Indeed, both rat species can be infected by *S. mansoni* in the laboratory. Whereas *R. rattus* permits the complete development of the parasite with egg release in the urine, *R. norvegicus* was found unable to expel the parasite eggs (Combes et al. 1975). A precluded compatibility of the black rat was then necessary for the transfer to occur.

### **3.2.3 Parasite adaptation**

Théron and Pointier (1995) suggested that epidemiological processes affected the genetic structure of the parasite populations. Their study highlighted the fact that two host-adapted populations of schistosomes co-exist, one adapted to the human host, the other to the murine host. Each can be distinguished by several characters as follows.

1. Three egg morphs of schistosomes have been distinguished, based on the shape of the egg and the lateral spine. Egg polymorphism was correlated with the level of participation of the murine host in schistosome circulation.
2. The frequency variation of the *ndh-1a* allele has allowed identification of three different groups of schistosomes, which also indicated a strong correlation between genetic differentiation and the implication of the black rat in the epidemiology of the disease.
3. The chronobiological polymorphism of the cercariae shed by snails also helped to define three schistosome groups, with cercarial shedding correlating with rodent activity in the sylvatic foci.

## **3.3 Relevance of these two models**

These two examples of lateral transfer have occurred as a consequence of human activities, in particular, species introduction on islands. The invasion success is supposed to have some links with parasites. Torchin et al. (2004) showed that invasive species are usually less parasitized in their new areas than in their native areas but that they are also less parasitized than other species in the new areas. Indeed, rats are less parasitized on is-

lands than on the mainland. Moreover, invasive hosts may also successfully establish themselves and spread in new habitats because of high immuno-competence (Møller and Cassey 2004), which may explain why they are more tolerant of local parasites (Lee and Klasing 2004). The immuno-competence hypothesis remains to be tested in the case of the black rat.

The recent confrontation of parasites and rodents offers interesting models for co-evolutionary studies, i.e. the evolution of parasite virulence and host resistance. Both parasite species respond to their new host (the black rat) and their new insular environment by changes in their life-history traits (egg size, size at maturity) and life cycle (shedding behaviour). However, adaptation and, in particular, resistance of the black rat to their new parasites appear to be limited. One provisional conclusion is that the co-evolutionary processes in the recently established host-parasite associations seem to be asymmetric and biased in favour of the parasites. These two examples highlight the importance of evaluating the role of parasites when dealing with invasion and biological conservation (Prenter et al 2004; Christe et al., this volume).

#### **4 Conclusion: the vulnerability of insular communities**

Human alteration of the global environment has triggered the sixth major extinction event in the history of life and caused widespread changes in the global distribution of organisms. These changes in biodiversity alter ecosystem processes and resilience of ecosystems to environmental perturbation (Chapin et al. 2000).

Invasive species are the second cause, after habitat fragmentation, of species extinction. The number of species introductions is expected to increase dramatically in the coming years as a result of accelerating international trade, making the control of biological invasions a priority (Lee and Klasing 2004).

Island populations have a much higher risk of extinction than mainland populations. Recorded extinctions since 1600 show that a majority of extinctions concerns insular animals and plants, although island species represent only a fraction of total species richness. For example, only 20% of all bird species are endemic on islands, but 90% of bird species driven to extinction in historic times were island dwellers (Myers 1979; Frankham 1997). Human activities (over-exploitation, habitat loss, and introduced species) have been the major cause of species extinction on islands in the past 50 000 years. The relative importance of each factor varies according to the taxonomic group, over-exploitation and introduced species being the

most important causes for vertebrates (Olson 1989). There is also a growing suspicion that new and modified diseases represent a significant factor (Frankham 1997).

The reasons why insular species are particularly prone to extinction or endangerment are still controversial:

1. Frankham (1997) has suggested that most island populations have low genetic variation because of founder effects and low population size. Genetic variation is the raw material for evolutionary change and allows populations to evolve in response to environmental changes such as human perturbations. Thus genetic impoverishment could favour greater sensitivity to perturbations.
2. Endemic insular species are unable to cope with stochastic effects (human perturbations, climatic events) because of their small population size, especially on small islands.
3. Many endemic island species are facing an increased risk of encountering new pathogens that are introduced through human activities.

Insular species are especially vulnerable to these non-native parasites.

The decrease in parasite species richness could be the first explanation for this higher vulnerability of insular populations to invasive pathogens. Hochberg and Møller (2001) argued that the insular epidemiological context should reduce host resistance to parasites and parasite virulence. Ecological immunology can provide crucial clues concerning this question (Lee and Klasing 2004; Lindström et al 2004). Specifically, a major challenge for future researchers will be to understand how immunology and physiology make an animal population more susceptible to pathogens (see Degen, Barnard and Benhke, Weil et al. in this volume).

Some recent studies assessed genetic diversity for a locus of the major histocompatibility complex (MHC) in insular small mammals (mainly murid) populations compared to mainland populations (Seddon and Baverstock 1999; Goüy de Bellocq et al. 2005; see Charbonnel et al. in this volume), suggesting that MHC diversity is not directly linked to insularity but rather to parasite diversity (Goüy de Bellocq et al. unpubl.).

Lindström et al. (2004) tested the hypothesis that investment in immune defence is influenced by parasite-mediated selection. They analyzed immune response of birds in relation to island size and parasite load and found that parasite prevalences and infection intensities increase with island size. Moreover, birds on large islands have increased concentrations of natural antibodies and raised a strong specific antibody response faster than birds on smaller islands. In contrast, the magnitude of cell-mediated immune responses decreases with increasing parasite pressure, i.e. on larger islands. Lindström et al. (2004) report results that are consistent with

the hypothesis that different immunological defence strategies are optimal in parasite-rich and parasite-poor environments.

Lindström et al. (2004) illustrated how various immunological strategies depend on the parasite context, but this does not allow us to determine if parasite-poor environments or parasite-rich ones are more vulnerable to a non-native parasite introduction. Changes in parasite assemblages, species richness, population densities and genetic diversity, all have numerous consequences for the evolution (or extinction) of insular species. Some of these changes have been quantified but much of them must be evaluated in further investigations.

The increasing problem of host invasion and parasite invasion is not restricted to island situations. Island populations constitute the most extreme case of species vulnerability, and the processes that operate on islands are of great significance to managing the risks due to human activities. Invasion and extinctions on islands are the first steps of what may occur everywhere else.

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